THE GENERA *DICYNODON* AND *DIICTODON* AND THEIR BEARING ON THE CLASSIFICATION OF THE DICYNODONTIA (REPTILIA, THERAPSIDA)

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(With 30 figures and 1 table)

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ABSTRACT

The Late Permian dicynodont genera *Dicynodon*, *Oudenodon*, *Diictodon* and *Kingoria* are diagnosed on the basis of skull details seen in the primary type material. Many of the species previously included under *Dicynodon* have been referred to other genera, but no attempt at assessing the validity of these types at the species level has been made. *Diictodon* has the greatest stratigraphical range among the four genera, occurring throughout the three zones of the Lower Beaufort of the South African Karoo, while the characteristic features of *Dicynodon* can be identified in modified form in a number of Triassic genera. *Dicynodon* and *Oudenodon* appear to be more closely related to each other than to *Diictodon*. *Kingoria*, with several unusual features in the palate and lower jaw, holds the least in common with other Late Permian genera. Recognition of the characters distinguishing the four genera from each other should aid future studies on the systematics and evolution of this important therapsid group.

CONTENTS

INTRODUCTION

The infra-order Dicynodontia represents a Late Permian and Triassic radiation of herbivorous therapsids. Its first appearance in the lowermost *Tapinocephalus* Zone of the South African Karoo's Beaufort Group coincides

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with that of the earliest known South African land vertebrates. Although dicynodonts, mainly of Triassic age, are now known from east Africa, India, China, Antarctica, Europe, and North and South America, the most complete record of the group is the South African one against which the other more restricted occurrences must be compared.

The evolution of the Dicynodontia, as far as can be traced in features of the skull morphology, chiefly involved numerous modifications of a basic innovation of the feeding process, and in terms of general skull structure the earliest and latest known representatives of the infra-order are essentially similar. Chief among the departures from the primitive condition are the tendency for replacement of the upper and lower dentitions by horny beaks, the establishment of a sliding quadrate-articular jaw joint, and the lateral migration of a portion of the external jaw adductor musculature to a new site of origin on the lateral surface of the temporal arch.

The dicynodont skull is consequently a highly distinctive one, and from the time of its original description by Owen (1845*a*) has frequently been described and figured in its many variations. However, the great abundance of specimens collected from numerous Beaufort localities, and the preference for detailed skull roof characters shown in the taxonomic work of earlier palaeontologists, combined to create a large number of poorly diagnosed dicynodont 'species' divided among a number of 'genera' of doubtful validity. In the bibliographic work of Haughton & Brink (1954), which takes into at least partial account revisions by Van Hoepen (1934) and Toerien (1953), no fewer than 111 South African species are assigned to the catch-all genus *Dicynodon*. Since the bulk of these dicynodonts is known from the Permian part of the Beaufort succession, it is among these forms that the taxonomic confusion is at its worst.

It has long been recognized that this state of affairs has served to obscure the potential importance of the Dicynodontia in a variety of fields of study. Attempts at rectifying the situation have resulted in a number of detailed studies on selected dicynodont groups; the cranial morphology of *Placerias* (Camp & Welles 1956), *Kingoria* (Cox 1959), *Daptocephalus* (Ewer 1961), *Lystrosaurus* (Cluver 1971), and *Oudenodon* (Keyser 1975) is now well known and these genera serve as standards of comparison with other forms.

Following the work of Toerien (1953), more attention has been paid to details of the palate and lower jaw (e.g. Cluver 1970, 1974*a*, 1974*b*, 1975; Keyser 1975). Cluver (1970) recognized previously undescribed cranial features in specimens of Permian age identified as *Dicynodon testudirostris*. Subsequent comparisons have shown that these features are not present in the type specimen (BMNH 36233) of *Dicynodon lacerticeps*, upon which Owen's (1845*a*) original description of *Dicynodon* was based. Rather, they are found in the type specimen (AMNH 5308) of *Diictodon galeops* Broom, 1913. It is now clear that the genus *Diictodon* is valid and distinct from *Dicynodon*, has greater stratigraphical and geographical ranges than previously suspected, and is abundant in certain Upper Permian Karoo localities (Cluver & Hotton 1979). Furthermore, comparisons based on type material confirm the validity of the genera *Oudenodon* and *Kingoria*, as revised and defined by Keyser (1975) and Cox (1959) respectively. In the following sections, expanded diagnoses of these two genera are included to allow full comparison with *Dicynodon* and *Diictodon*. Diagnoses of these four important dicynodont genera help to remove much of the uncertainty surrounding the status of the type specimens currently assigned to *Dicynodon*. Locality and stratigraphic information with respect to type specimens has been taken from Haughton & Brink (1954) and Kitching (1970, 1977). The latter author's division of the Permian part of the Beaufort group into *Tapinocephalus*, *Cistecephalus*, and *Daptocephalus* zones is followed.

GENERAL SKULL MORPHOLOGY

The highly distinctive skull structure of dicynodonts (Figs 1–9) is modelled around a jaw mechanism unique among tetrapods. The preorbital portion of the skull is short, and the temporal region expanded to accommodate a greatly enlarged temporal musculature. The temporal muscles arose medially from a broad, flat process of the postorbital that covers much of the parietal in most forms.

The highest areas of origin are marked by bony parietal ridges which in some dicynodonts meet in the midline to form a longitudinal crest behind the parietal foramen. Lateral portions of the temporal muscles arose from a flattened zygoma formed chiefly by the squamosal, and posterior portions from a laterally expanded process of the squamosal that slants downward and forward with respect to the zygoma.

The quadrate is inserted into the distal end of the ventral process of the squamosal and is covered laterally by the quadratojugal (Figs 3–4). In lateral aspect the squamosal process appears to be suspended from the back of the skull, and its function as a support for the quadrate and an origin for jaw muscles is most accurately reflected by the term suspensorium.

The lateral expansions of the squamosals give a plate-like configuration to the otherwise rather massive occiput (Fig. 8). The bones shared between the occiput and the short, stout basis cranii tended to fuse very early in life.

The jaws (Figs 3, 7–9) are short, stout, beak-like and generally toothless. In the upper jaw the premaxillae are fused in the midline and firmly sutured to the maxillae and more posterior parts of the palate. In the lower jaw the dentaries are fused at the symphysis, which is remarkably robust and deep. Coronoid bones are lacking and prominent coronoid processes are seldom developed on the dentaries. In life, the temporal musculature slanted sharply forward from its origins in the temporal fossa to insert on the coronoid region and on the lateral face of the dentary, about half-way between the articulation of the lower jaw and the tip of the symphyseal beak. In some forms the lateral part of the insertion, which is bounded dorsally by the coronoid margin of the dentary and ventrally by the mandibular fenestra, is expanded laterally into a shelf-like structure (lateral shelf, Crompton & Hotton 1967) (Figs 3, 8). Deeper portions

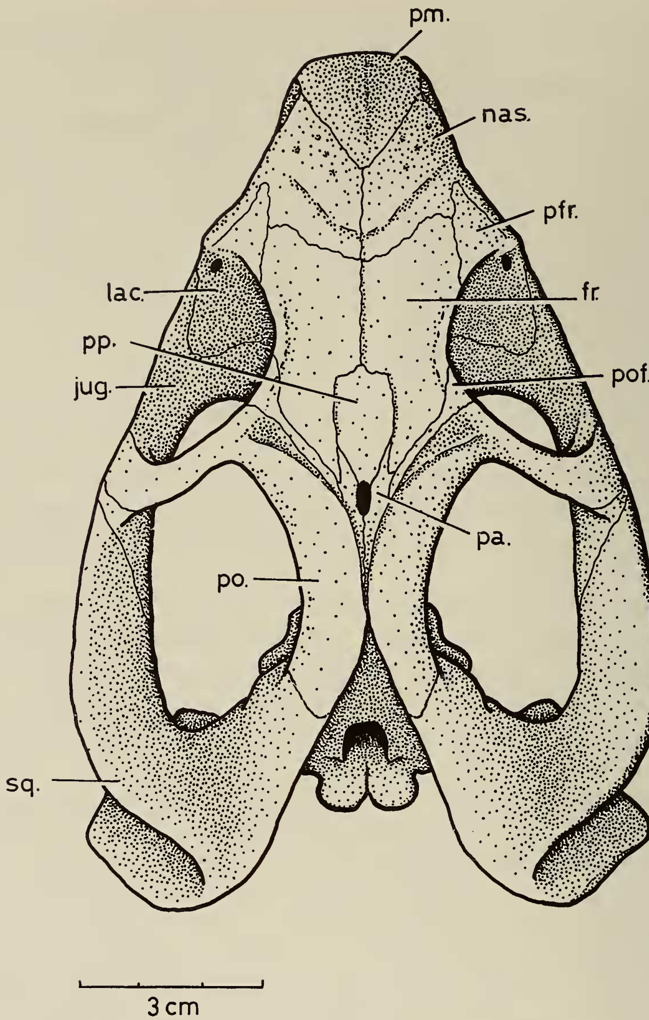

Fig. 1. *Dicynodon* sp. SAM–B88. Skull in dorsal view.

of the temporal musculature inserted inside the jaw ramus, in and around the adductor (Meckelian) fossa (Cluver 1974*a*, 1975).

The articulation of the lower jaw is unique in that both bearing surfaces are essentially convex (Figs 3, 7, 9), that of the articular being about twice as long as that of the quadrate. This can be construed as clear evidence of longitudinal sliding of the lower jaw during the bite, and the angle at which muscular force was applied shows that the motion during which the bite was most effective was one of retraction.

The toothless margins of the premaxillae and maxillae are usually sharp-edged. Except in *Endothiodon* and its closest allies, the middle of the maxilla is

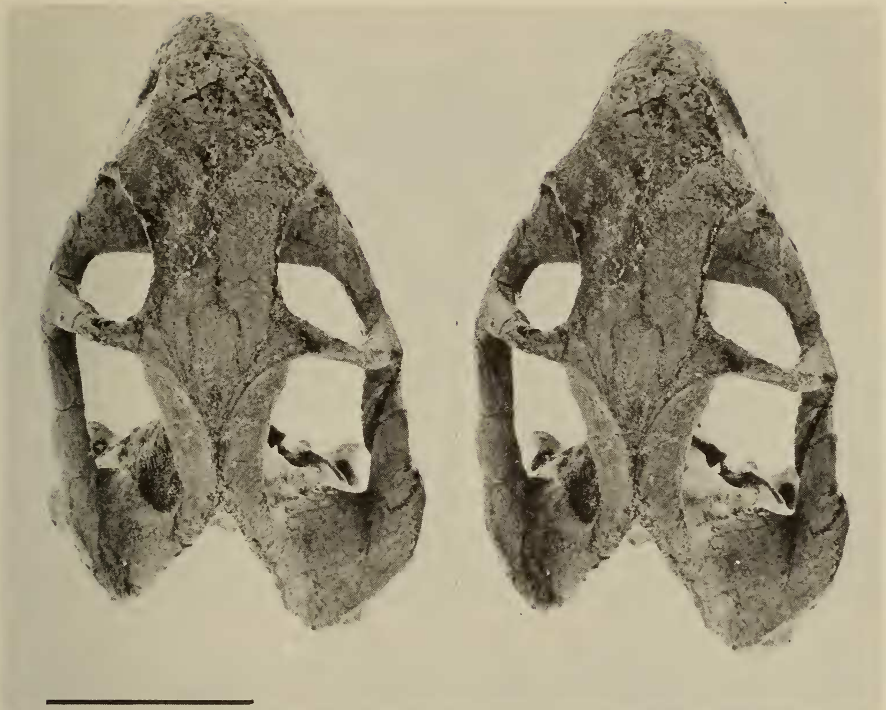

Fig. 2. *Dicynodon* sp. SAM–B88. Stereophotograph of skull in dorsal view. Scale: 5 cm.

thickened and produced downward as a caniniform process. Because of its thickness the caniniform process is triangular in cross-section presenting lateral, medial and posterior surfaces. In those forms in which it is present, the tusk erupts from the ventromedial surface of this process. In some forms, small non-caniniform teeth erupt from the flat medial surface of the maxilla (and in some cases from the premaxilla as well). A secondary palate, analogous to that which is found in cynodont mammal-like reptiles and mammals, is present and consists chiefly of a broad, plate-like posterior expansion of the fused premaxillae.

A finely-punctate sculpture is developed on the anterior and dorsal surfaces of the dentary symphysis, on the external surfaces of the premaxillae and palatines (in most forms), and on most external surfaces of the maxillae. It may be assumed that during life these surfaces were covered by horn because of their resemblance to bone surfaces that are covered by horn in living turtles and birds.

The three-sided caniniform process exhibits sculpture on its medial and lateral surfaces, but its posterior surface is smooth. The large masticatory muscles passed just behind the posterior surface, the smoothness of which suggests a place of attachment for a large and muscular *Mundplatte*, which in life lay in front of the temporal musculature in the corner of the mouth (Cluver 1975). The posterior surfaces of the caniniform processes thus provide useful

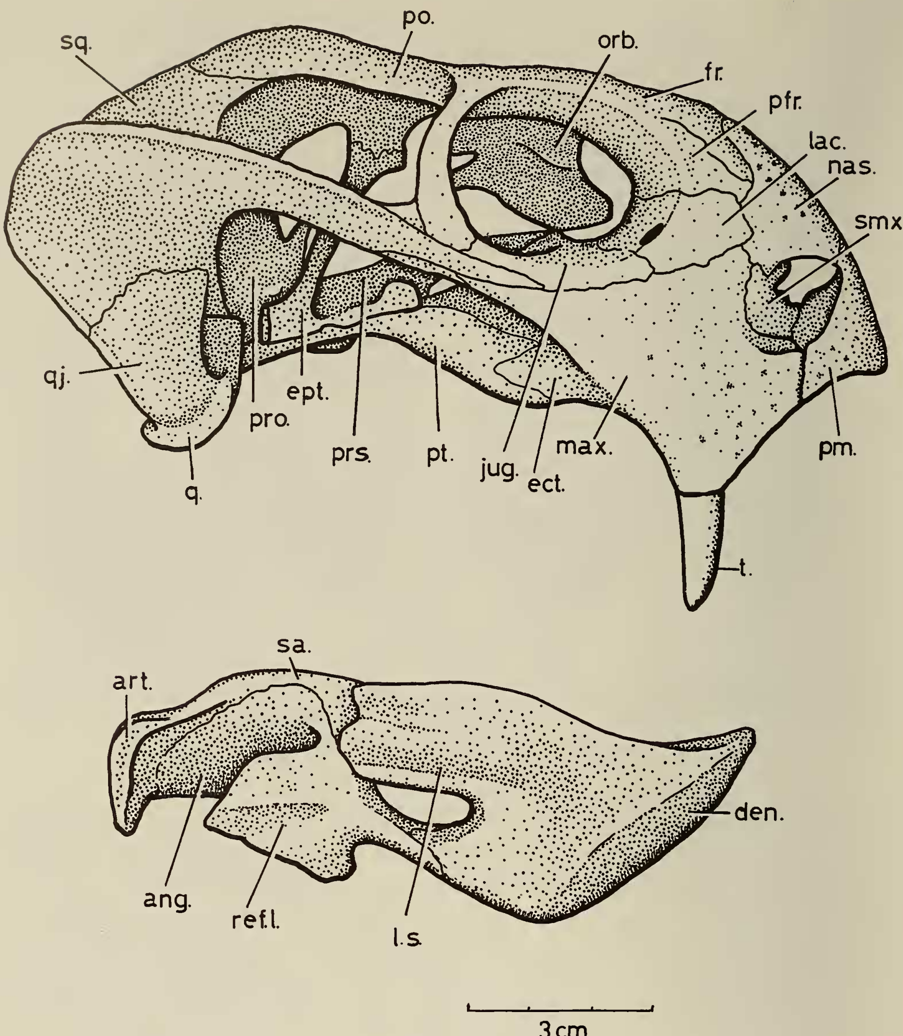

Fig. 3. *Dicynodon* sp. SAM–B88. Skull and lower jaw in lateral view.

landmarks for the corners of the mouth, and the mouth opening can be delimited posteriorly by a line drawn between the medial sides of the backs of the caniniform processes at the general level of the ventral margins of the premaxillae. The posterior margin of the mouth, defined here in functional terms, corresponds closely to that defined by Cruickshank (1968) on more exclusively anatomical grounds, i.e. the front of the choanae.

As confirmed by Agnew (1959), the skull is akinetic, and premaxillae, maxillae, palatines, pterygoids and ectopterygoids are firmly knit in the palate. In addition, the pterygoids are so closely and complexly sutured to the basis cranii a little behind their midlength (Olson 1944) (Figs 5–6) that, except in serial section, they appear fused to it.

The blade-like palatine rami of the pterygoids are elongate and oriented anteroposteriorly; there are no transverse pterygoid flanges. Between them the palatine rami enclose a deep, rather broad vault, into the front of which the choanae open. Anteriorly this vault, which may be termed the interpterygoid fossa, is partially roofed by the vomers and dorsal wings of the palatines (Fig. 5). The vomers enter the interpterygoid fossa as a single midline structure arising from the back of the premaxilla between the choanae, and bifurcate posteriorly at a variable distance behind the secondary palate. This bifurcation forms the anterior margin of the variably narrow fusiform or ovoid interpterygoid vacuity, which pierces the roof of the interpterygoid fossa. Through the interpterygoid vacuity the ventral edge of the slender parasphenoid rostrum may be seen in well-preserved and carefully prepared skulls. Only the interpterygoid vacuity, so restricted, is homologous with the phylogenetically ancient interpterygoid vacuity of less specialized reptiles and anthrocosaurian amphibians, and presumably was inherited with little change from such ancestors. The interpterygoid fossa, which has come to surround the interpterygoid vacuity, is a new entity formed in dicynodonts by rearrangement of the palatine rami of the pterygoids

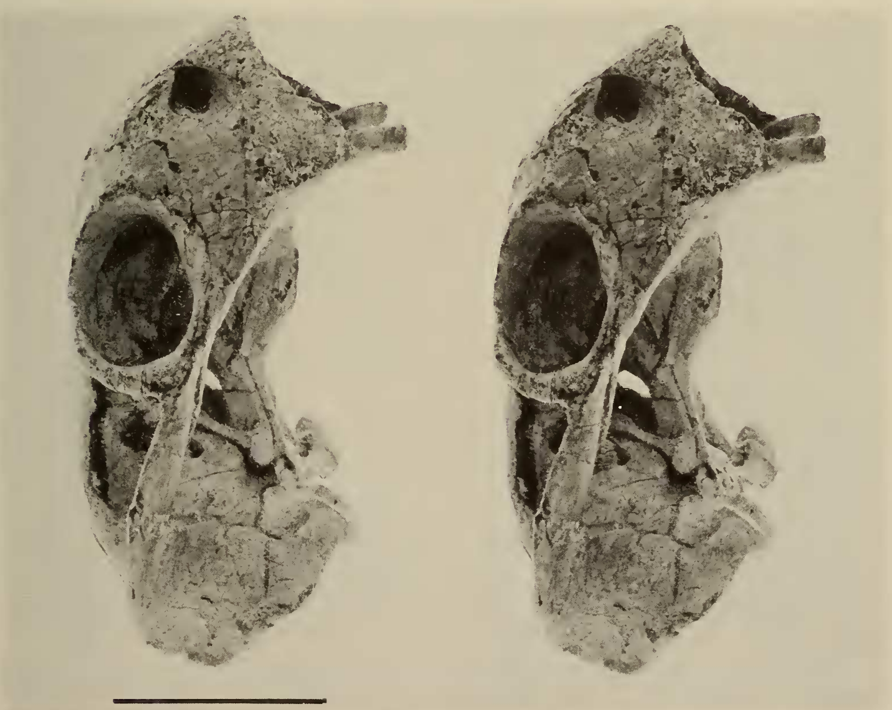

Fig. 4. *Dicynodon* sp. SAM–B88. Stereophotograph of skull in lateral view. Scale: 5 cm.

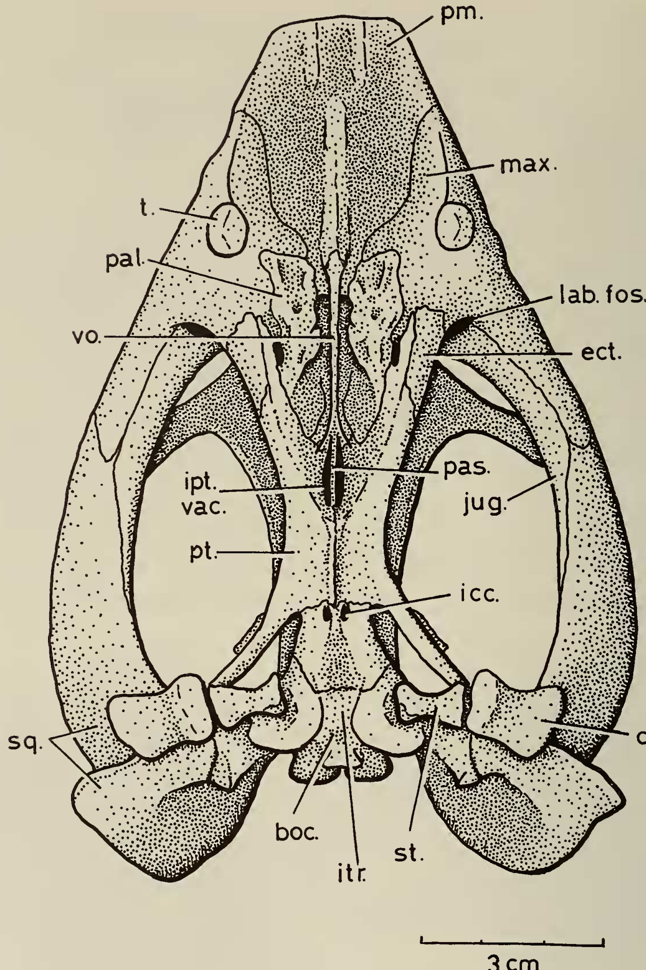

Fig. 5. *Dicynodon* sp. SAM–B88. Skull in ventral view.

and the formation of a secondary palate. The fossa is as distinctive of dicynodonts as the structure and function of their peculiar jaw articulation, to which its development is probably closely related.

THE GENUS *DICYNODON* (Figs 1–11)

Dicynodon Owen

Diagnosis

Medium-sized to large dicynodonts (average skull length 100 mm to over 400 mm), single pair of maxillary tusks in upper jaw, lower jaw edentulous. Postorbitals tend to cover parietals behind parietal foramen. Septomaxilla merges smoothly with outer surface of snout, does not meet lacrimal. Low boss formed over external nares by nasals. Caniniform process of maxilla arises as ventral extension of palatal rim. Palatal rim sharp-edged, uninterrupted by notch. Palatal portion of palatine large, makes short contact with premaxilla. Vomers form long, narrow septum in interpterygoid fossa, interpterygoid vacuity short. Ectopterygoid small, displaced laterally. Labial fossa present between maxilla, palatine and jugal. Pterygoid makes short contact with maxilla. Basioccipital tubera separated by intertuberal ridge. Fused dentaries carry narrow dentary tables .dorsal edge of dentary carries deep sulcus behind dentary tables. Rear of dentary extended dorsally to form weak coronoid process. Mandibular fenestra large, bounded dorsally by lateral dentary shelf.

Dicynodon lacerticeps Owen

Dicynodon lacerticeps Owen, 1845*a*: 59, pls 3–4.

Type specimen

Skull and lower jaw, BMNH 36233.

Locality

Tarka prolongation of the Winterberg, Cape Province.

Fig. 6. *Dicynodon* sp. SAM–B88. Stereophotograph of skull in ventral view. Scale: 5 cm.

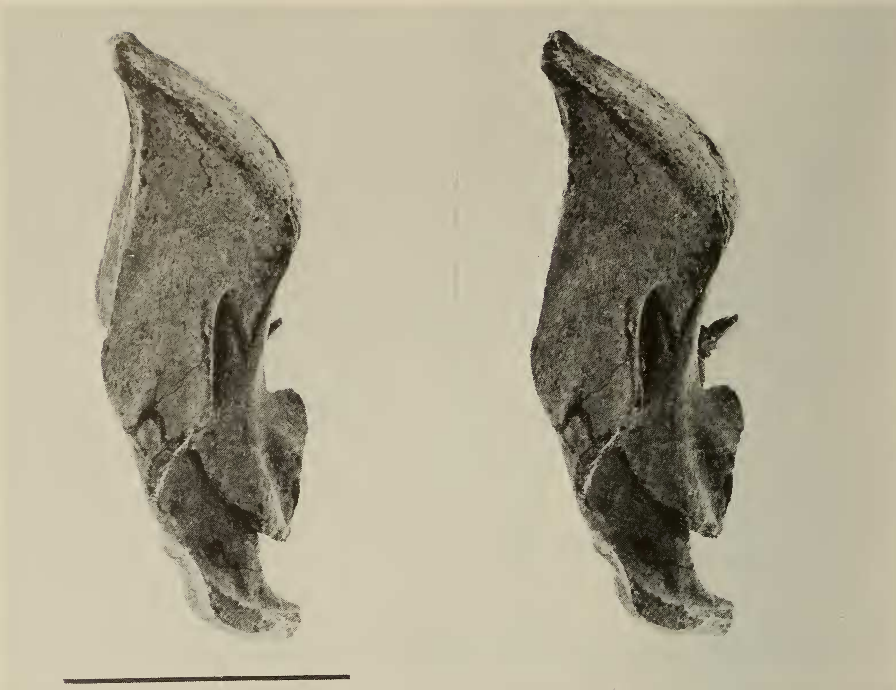

Fig. 7. *Dicynodon* sp. SAM–B88. Stereophotograph of lower jaw in lateral view. Scale: 5 cm.

Horizon

Daptocephalus Zone.

Diagnosis

As for genus.

Remarks

Owen published two accounts of *Dicynodon lacerticeps* in 1845, both based on a lecture delivered by him before the Geological Society of London on 8 January of that year. The paper which appeared in the *Transactions of the Geological Society* (Owen 1845*a*) with illustrations of the fossil specimens is regarded as having priority here; in a subsequent paper in the same journal Owen (1856: 233) refers to this description as 'my former account' of the new forms. The paper which appeared in the *Proceedings of the Geological Society* (Owen 1845*b*) is a shortened version of the *Transactions* article.

One reason for the uncertainty surrounding the status of the many described species of *Dicynodon* is the poor preservation of the type specimen of *Dicynodon lacerticeps* itself (Figs 10–11). The specimen is a fairly complete skull and lower jaw, but much of the surface bone is damaged and sutures are subsequently difficult or impossible to trace. However, recent preparation has exposed several

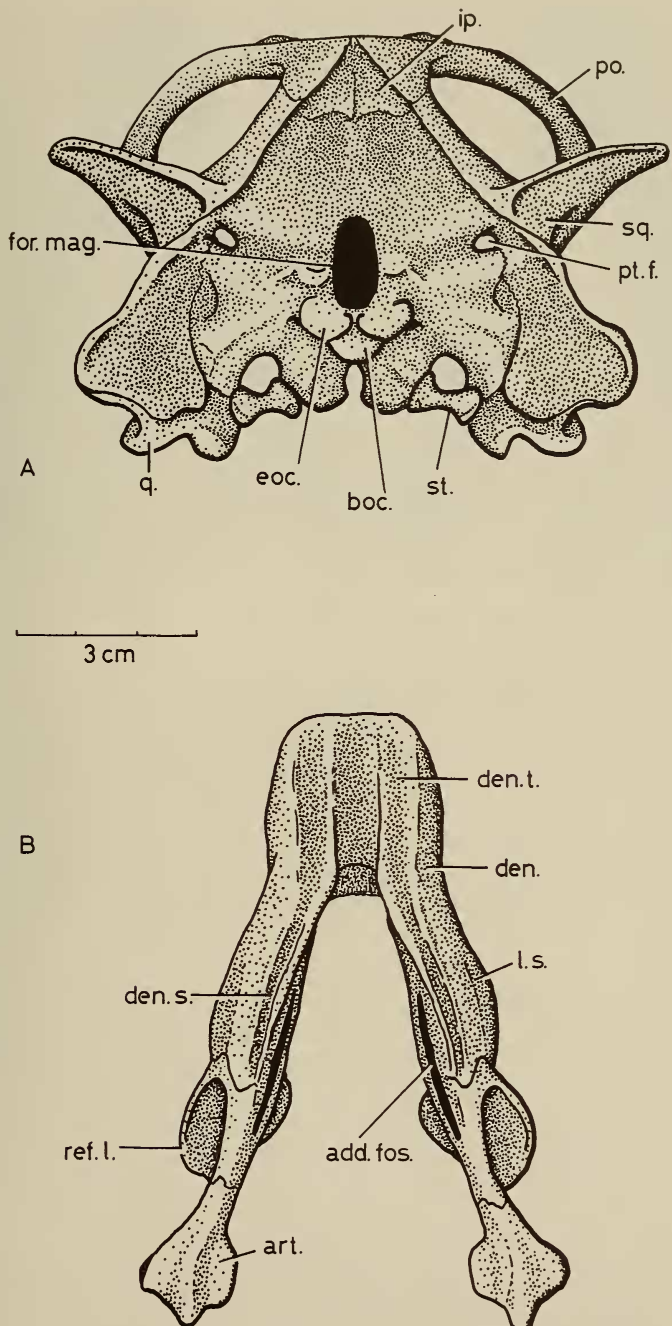

Fig. 8. *Dicynodon* sp. SAM–B88. A. Occipital view of skull. B. Lower jaw in dorsal view.

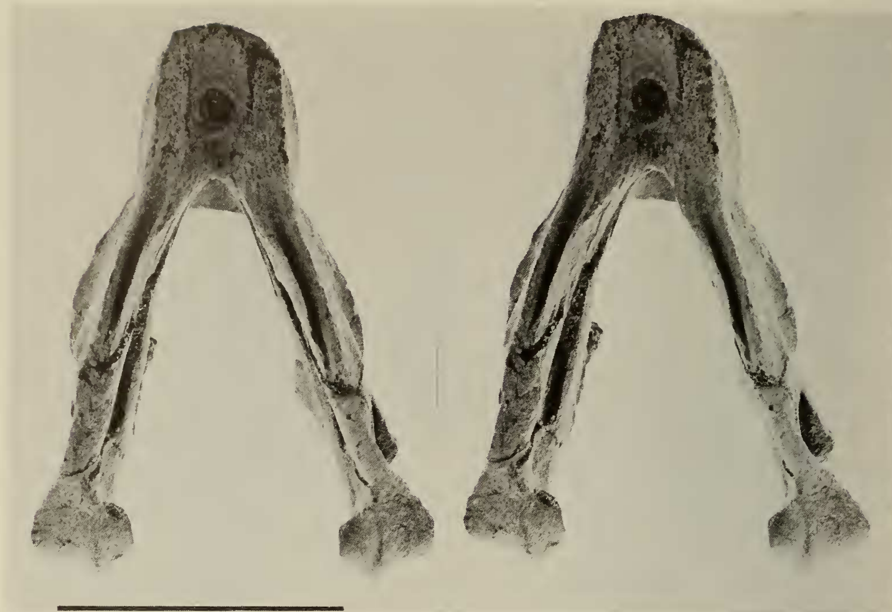

Fig. 9. *Dicynodon* sp. SAM–B88. Stereophotograph of lower jaw in dorsal view. Scale: 5 cm.

key areas of the skull and enough can now be seen to distinguish it from other dicynodont genera founded on better type material.

The dorsal skull surface is gently curved from the parietal region to the tip of the snout, and in lateral view the skull appears relatively deep. The postorbitals approach each other very closely behind the parietal foramen, but may be separated by a thin parietal crest. A large, leaf-like preparietal and a clear postfrontal are present, as well as a relatively small prefrontal. The prefrontal may be separated from the lacrimal on the side of the snout by a narrow posterior process of the nasal, but poor preservation does not allow confirmation of this point.

The sharp-edged palatal rim is continued on to the anterior part of the caniniform process without interruption, and in lateral view forms a continuous arc. A pair of powerful maxillary tusks are present, as are two anterior premaxillary ridges on the palatal surface of the premaxilla. Matrix obscures the area where the more posterior, median ridge is normally found in dicynodonts.

The basioccipital tubera are joined by a raised area of the basicranium, the intertuberal ridge, as seen in *Lystrosaurus* (Cluver 1971). The deepest part of the ridge is on the basioccipital, behind the basioccipital-basisphenoid suture. Only the rear of what appears to have been a wide interpterygoid vacuity is preserved. The palatines are large, but their anterior palatal portions are partly obscured and their relationships with the maxillae and premaxillae cannot be determined.

In the poorly preserved lower jaw, dentary tables are present and the dorsal edge of the dentary appears to be excavated in the form of a longitudinal sulcus.

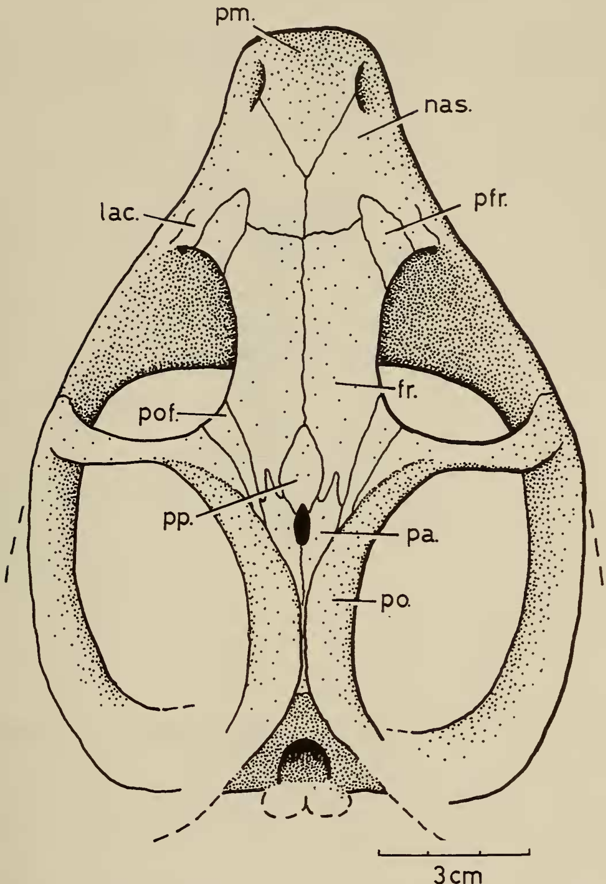

Fig. 10. *Dicynodon lacerticeps* BMNH 36233. Type specimen. Skull in dorsal view, partially reconstructed and with distortion corrected.

In spite of the poor condition of the type specimen, the combination of characters which can be determined in it is sufficient to permit referral of additional, fully preserved specimens (Figs 1–9) to *Dicynodon lacerticeps* and to allow the formulation of a full generic diagnosis. The species listed below may be retained in the genus *Dicynodon* on the basis of type material; an analysis of the validity of these species is beyond the scope of this generic-level revision, but future work will undoubtedly result in the establishment of a smaller number of valid species.

Dicynodon testudiceps Owen

Dicynodon testudiceps Owen, 1845*a*: 71, pls 5–6.

Type specimen

Anterior part of skull, BMNH 47051.

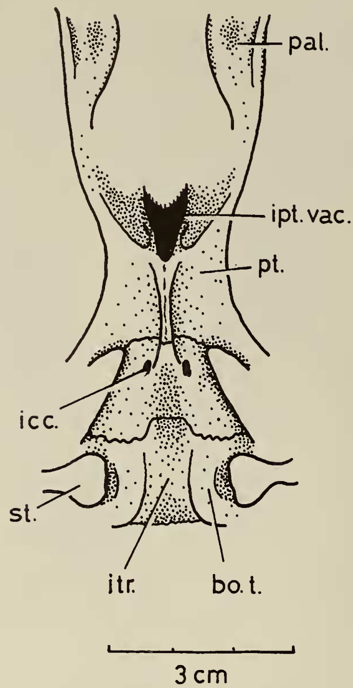

Fig. 11. *Dicynodon lacerticeps* BMNH 36233. Type specimen. Partial ventral view of skull, distortion corrected.

Locality

Fort Beaufort, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon leoniceps Owen

Dicynodon leoniceps Owen, 1876: 32, pls 24–26.

Type specimen

Skull, BMNH 47047.

Locality

Gats River, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Van Hoepen (1934) proposed this species as the type of a new genus, *Daptocephalus*. Comparison of the type specimen with the type of *Dicynodon lacerticeps* shows that large size is the only feature that can be used to distinguish

Daptocephalus from *Dicynodon*. The species *leoniceps*, which may prove to be a valid one, is accordingly reassigned to *Dicynodon*.

Dicynodon lissops Broom

Dicynodon lissops Broom, 1913: 450, fig. 11.

Type specimen

Skull, AMNH 5508.

Locality

Wilgerbosch, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon leontops Broom

Dicynodon leontops Broom, 1913: 451, fig. 12.

Type specimen

Skull AMNH 5582.

Locality

Bethulie, Orange Free State.

Horizon

Daptocephalus Zone.

Dicynodon alticeps Broom & Haughton

Dicynodon alticeps Broom & Haughton, 1913: 37, pl. 7.

Type specimen

Skull, SAM–2347.

Locality

Dunedin, Beaufort West district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon watsoni Broom

Dicynodon watsoni Broom, 1921: 653, fig. 32.

Type specimen

Skull, SAM–7849.

Locality

East of New Bethesda, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon gilli Broom

Dicynodon gilli Broom, 1932: 176, fig. 60.

Type specimen

Skull, SAM–4008.

Locality

Watervlei, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon venteri Broom

Dicynodon venteri Broom, 1935*b*: 69, fig. 10.

Type specimen

Skull, TM 199.

Locality

New Bethesda, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon validus Broom

Dicynodon validus Broom, 1935*b*: 70, fig. 11.

Type specimen

Skull, TM 252.

Locality

Leeukloof, Beaufort West district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon microdon Broom

Dicynodon microdon Broom, 1936: 376, figs 22–23.

Type specimen

Skull, TM 267.

Locality

Bethesda Road, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon luckhoffi Broom

Dicynodon luckhoffi Broom, 1937: 306, fig. 6.

Type specimen

Skull, SAM–K1219

Locality

Zuurplaats, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon macrodon Broom

Dicynodon macrodon Broom, 1940*a*: 81, fig. 10A–B.

Type specimen

Skull, RC 22.

Locality

Grootfontein, Murraysburg district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon cadlei Broom

Dicynodon cadlei Broom, 1940*a*: 82, fig. 11.

Type specimen

Skull, RC 23.

Locality

Hoeksplaas, Murraysburg district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon calverleyi Broom

Dicynodon calverleyi Broom, 1940*b*: 179, fig. 21.

Type specimen

Skull, RC 39.

Locality

Klipfontein, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon grahami Broom

Dicynodon grahami Broom, 1940*b*: 180, fig. 22.

Type specimen

Skull, RC 39.

Locality

Klipfontein, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon trigonocephalus Broom

Dicynodon trigonocephalus Broom 1940*b*: 182, fig. 24.

Type specimen

Skull, RC 38.

Locality

Klipfontein, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon aetorhamphus Broom

Dicynodon aetorhamphus Broom, 1948: 605, figs 23A, 24A.

Type specimen

Skull, RC 85.

Locality

Hoeksplaas, Murraysburg district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon leontocephalus Broom

Dicynodon leontocephalus Broom, 1950: 246, fig. 1.

Type specimen

Skull, RC 96.

Locality

Springfontein (Springfield), Middelburg district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon clarencei Broom

Dicynodon clarencei Broom, 1950: 247, fig. 2.

Type specimen

Skull, RC 77.

Locality

Hanover, Cape Province.

Horizon

Cistecephalus Zone.

THE GENUS *OUDENODON* (Figs 12–17)

Oudenodon Owen

Diagnosis

Medium-sized to large dicynodonts (skull length ranging from 100 mm to over 300 mm), teeth lacking in both upper and lower jaws. Postorbitals well separated on skull roof by parietals. Septomaxilla recessed within external naris, lacrimal may extend forward above maxilla to posterior margin of naris. Nasal forms boss over naris. Maxilla carries weak caniniform process, with sharp-edged posterior crest. Palatal portion of palatine large, meeting posterior border of premaxilla. Vomers form short septum in anterior part of interpterygoid fossa, interpterygoid vacuity long and narrow. Basipterygoid region constricted. Ectopterygoid large, pterygoid does not contact maxilla. Dentaries carry narrow dentary tables, dorsal edge of dentary carries deep sulcus. Coronoid process weak or absent. Weak lateral dentary shelf above large mandibular fenestra.

Oudenodon baini Owen

Oudenodon baini Owen, 1860: 46, pl. 1 (fig. 1).

Type specimen

Skull lacking lower jaw, BMNH 36232.

Locality

Near Fort Beaufort, Cape Province.

Horizon

Cistecephalus Zone.

Diagnosis

As for genus.

Discussion

The almost complete type skull (Figs 12–15) has been fully prepared and detailed comparisons with other dicynodont taxa are possible. The most dis-

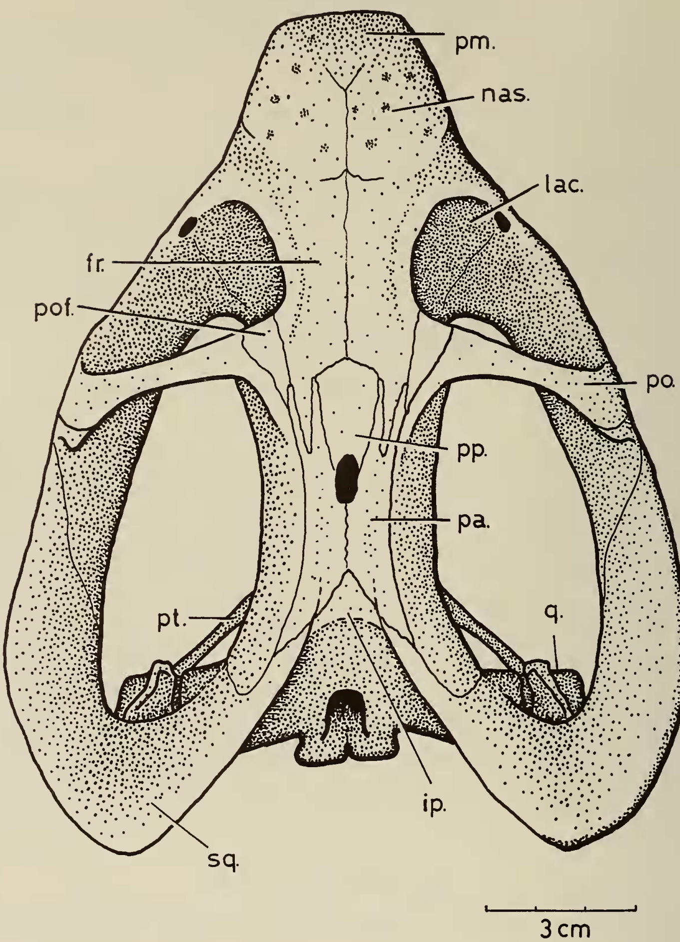

Fig. 12. *Oudenodon baini* BMNH 36232. Type specimen. Skull in dorsal view.

tinctive features in the palate are the long, narrow interpterygoid vacuity, the deep and relatively narrow secondary palate, the sharp maxillary crest behind the caniniform process, and the absence of maxillary tusks. These characteristics, taken together with the wide parietal exposure in the skull roof, are sufficient to permit referral of more fully preserved specimens to *Oudenodon* for inclusion of lower jaw features in the generic diagnosis.

In lateral view (Figs 15–16) the skull of *Oudenodon* is not as deep as that of *Dicynodon*, and the anterior surface of the short snout lies almost at right angles to the flat surface of the dorsal skull roof. The palatal rim in front of the caniniform process is blunt, but the usual pair of anterior premaxillary ridges is

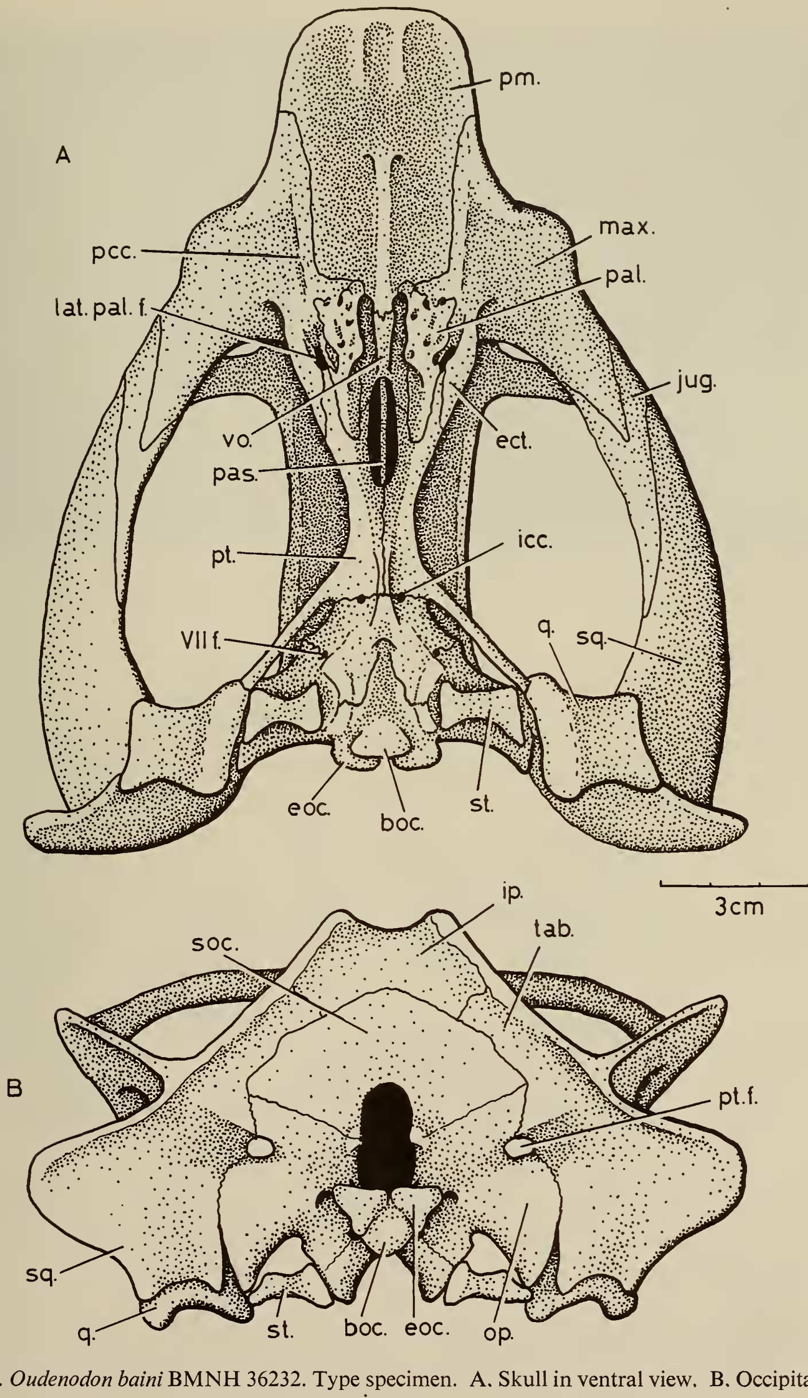

Fig. 13. *Oudenodon baini* BMNH 36232. Type specimen. A. Skull in ventral view. B. Occipital view.

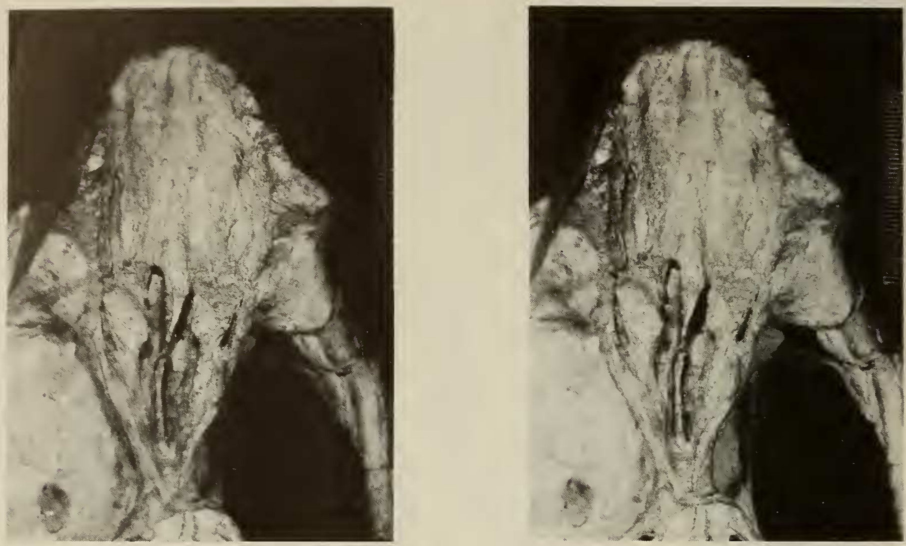

Fig. 14. *Oudenodon baini* BMNH 36232. Type specimen. Stereophotograph of palate. Scale: 8 cm.

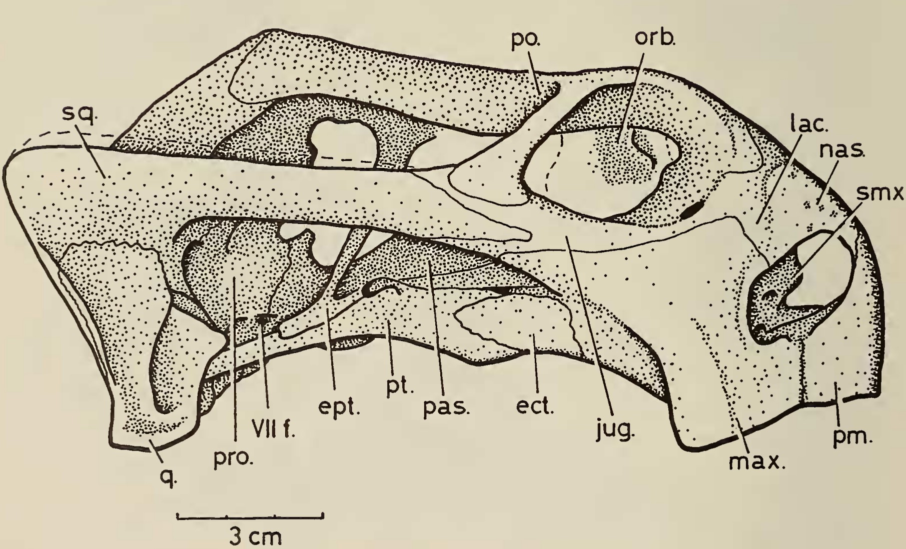

Fig. 15. *Oudenodon baini* BMNH 36232. Type Specimen. Skull in lateral view.

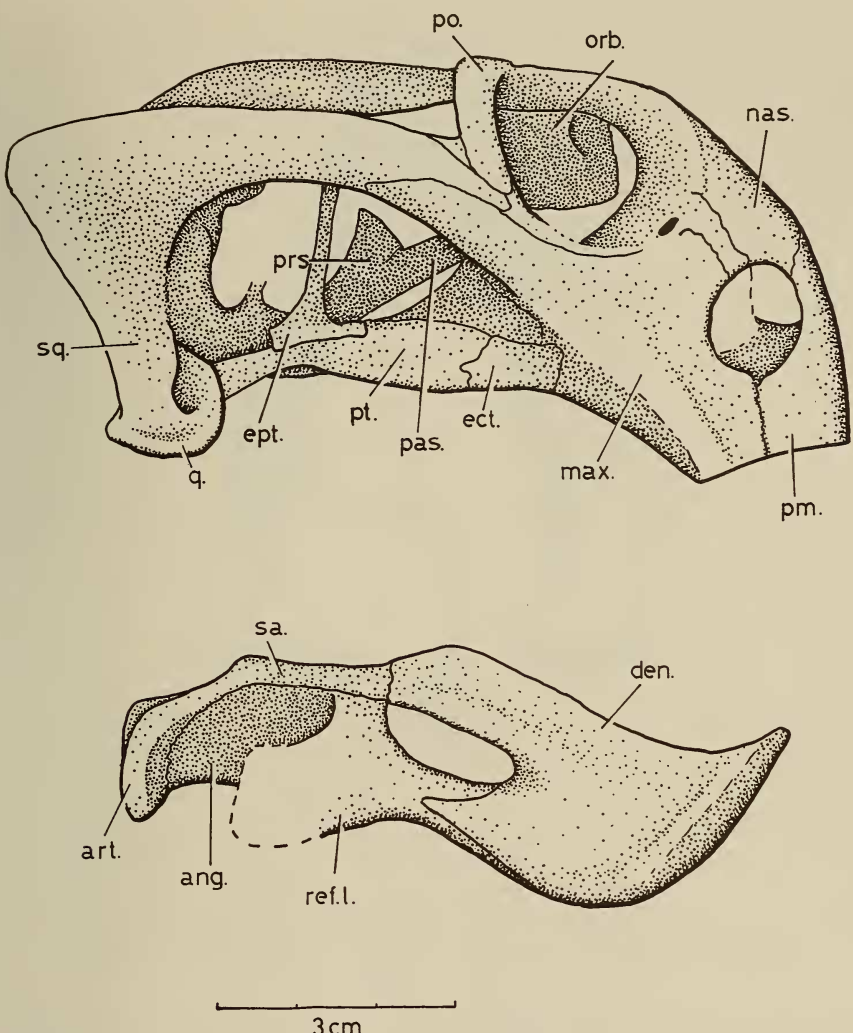

Fig. 16. *Oudenodon* sp. SAM–6045. Skull and jaw in lateral view.

present. In general shape and in the possession of dentary tables and a dorsal dentary sulcus, the lower jaw is essentially similar to that of *Dicynodon*.

Keyser (1975) has reviewed the species of *Oudenodon* and lists all type material fully; it is unnecessary to repeat the information here. Keyser recognizes only three species, these being *Oudenodon baini* Owen, *Oudenodon grandis* (Haughton), and *Oudenodon luangwaensis* (Boonstra) and suggests that the large number of other dicynodont types that can be assigned to the genus are synonyms of *Oudenodon baini*.

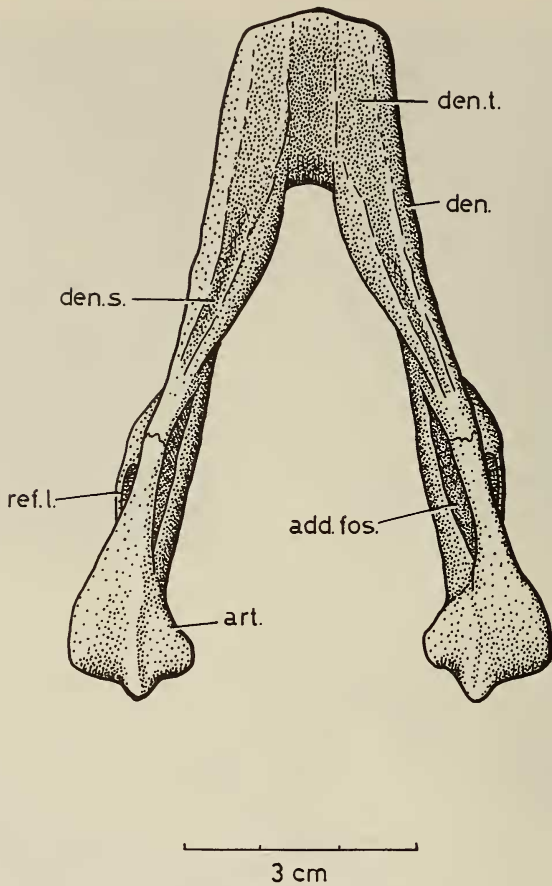

Fig. 17. *Oudenodon* sp. SAM–6045. Lower jaw in dorsal view.

THE GENUS *DIICTODON*

Diictodon Broom

Diagnosis

Medium-sized dicynodonts (average skull length 110 mm), jaws either lacking teeth altogether, or bearing a single pair of maxillary tusks. Postorbitals tend to cover parietals behind pineal foramen. Septomaxilla recessed within external naris, maxilla rises high in side of snout to meet the nasal. Nasal forms boss over external naris. Maxilla carries prominent caniniform process, clearly demarcated from anterior maxillary palatal rim. Sharp anterior edge of caniniform process set medially to anterior palatal rim. Palatal portion of palatine small, does not meet premaxilla. Vomers form short septum in interpterygoid

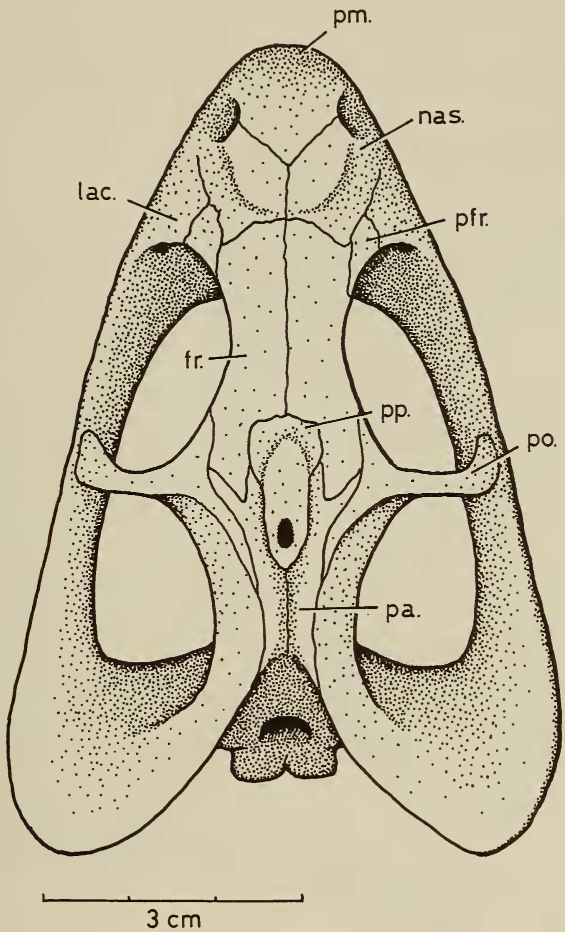

Fig. 18. *Diictodon galeops* AMNH 5308. Type specimen. Skull in dorsal view.

fossa. Interpterygoid vacuity long. Ectopterygoid large, separating pterygoid from maxilla. Fused dentaries carry wide dorsal dentary tables, with high medial borders. Rear of dentary table extended medial to level of inner surface of jaw ramus. Dorsal edge of dentary rounded behind dentary table, no coronoid process present. Mandibular fenestra large, no expanded lateral dentary shelf for insertion of adductor musculature.

Diictodon galeops Broom

Diictodon galeops Broom, 1913: 453, fig. 15.

Type specimen

Skull lacking lower jaw, AMNH 5308.

Locality

'Slachter's Nek', Somerset East district, Cape Province.

Horizon

Upper Permian, *Cistecephalus* Zone.

Diagnosis

Preparietal bone large, surrounding parietal foramen. Postfrontals absent, caniniform processes and maxillary tusks small. Parietals partially exposed between postorbitals behind parietal foramen.

Remarks

The type skull (Figs 18–21) is well preserved but lacks the lower jaw, quadrates and stapes. Small tusks are present. Distinctive features of the specimen are the inflated preparietal bone, which surrounds the parietal opening, and the absence of postfrontals on the skull roof. No septomaxillae can be seen, and it is likely that these bones became disassociated from the skull, as the stapes and quadrates evidently did, prior to fossilization.

The postorbitals approach each other behind the pineal opening but do not cover the parietals fully. The maxilla rises high in the side of the snout and meets the nasal so that the lacrimal is confined to the orbital border. In ventral view it can be seen that the base of the caniniform process is offset medially to the palatal rim in the form of an anteriorly facing blade, separated from the palatal rim by a clear notch (Figs 20–21). Besides the usual single median and double

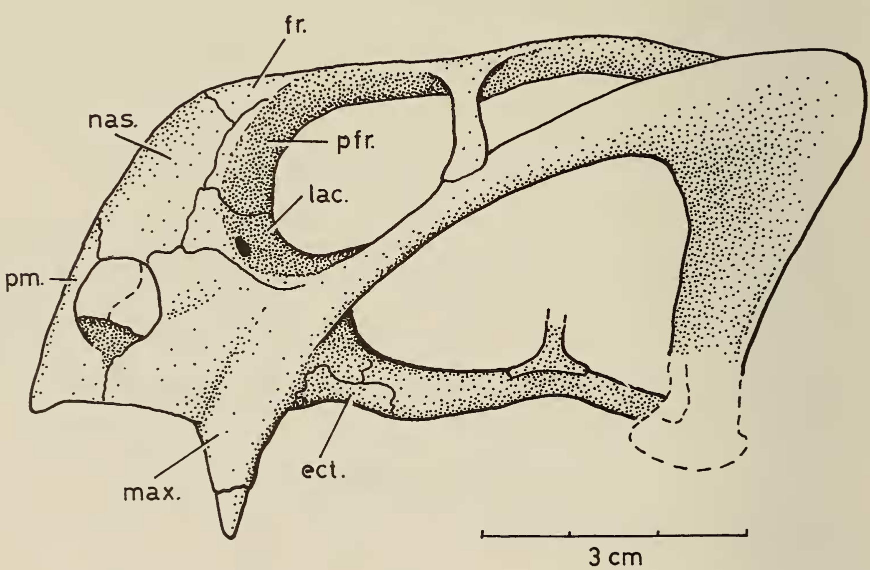

Fig. 19. *Diictodon galeops* AMNH 5308. Type specimen. Skull in lateral view.

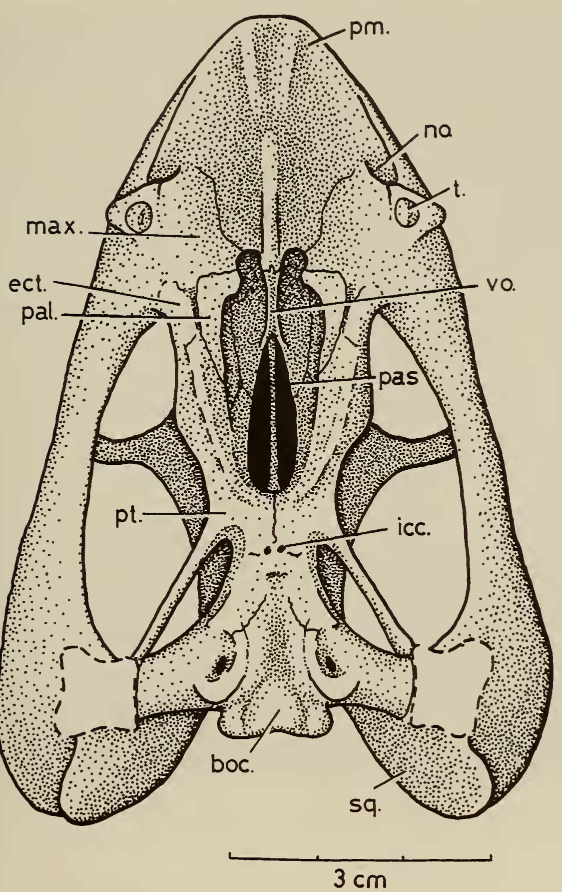

Fig. 20. *Diictodon galeops* AMNH 5308. Type specimen. Skull in ventral view.

anterior palatal ridges, there is a more lateral ridge on each side of the secondary palate, medial to the caniniform process. The palatal portion of the palatine is small, and does not meet the premaxilla. The long, wide interpterygoidal vacuity extends far forward to where the vomers unite and descend to meet the posterior spine of the premaxilla. The lateral pterygoidal borders of the interpterygoid fossa are strongly constructed, but there is no pterygoid-maxilla contact.

Diictodon feliceps (Owen)

Dicynodon feliceps Owen, 1876: 45, pl. 43.

Type specimen

Skull, BMNH 47052.

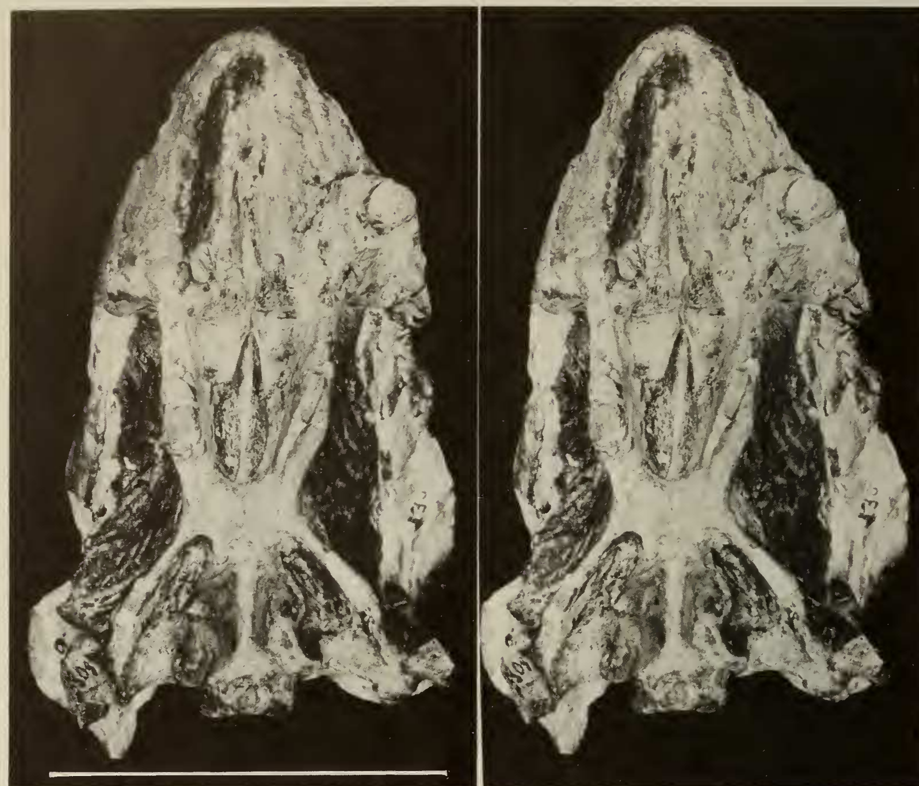

Fig. 21. *Diictodon galeops* AMNH 5308. Type specimen. Stereophotograph of palate. Scale: 5 cm.

Locality

Fort Beaufort, Cape Province.

Horizon

Cistecephalus Zone.

Diagnosis

Postorbitals cover parietals behind parietal foramen, parietal foramen not surrounded by preparietal. Narrow postfrontal exposed on dorsal skull roof. Caniniform process large, maxillary tusks present or absent.

Remarks

The species *feliceps* is the earliest described form which shows the characteristics of *Diictodon* as diagnosed above, but examination of dicynodont type material shows that a number of other described species of *Dicynodon*, including

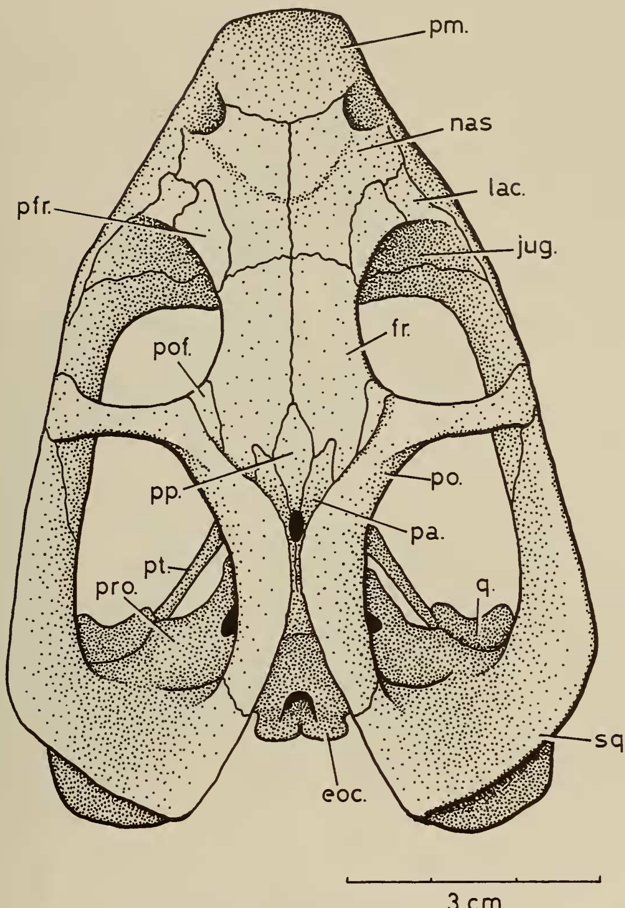

Fig. 22. *Diictodon testudirostris* SAM–10086. Skull in dorsal view.

D. testudirostris (see Cluver 1970), closely resemble the species *feliceps* and can be referred to the genus *Diictodon* (Figs 22–26).

An analysis of the validity of these species is outside the scope of the present generic level revision and, as in the case of *Dicynodon* and *Oudenodon*, the list below is compiled only on the basis of type material which can be included under *Diictodon*. Future investigations may well result in a smaller number of recognizable species.

Diictodon jouberti (Broom)

Dicynodon jouberti, Broom, 1905: 331.

Type specimen

Skull, SAM–695.

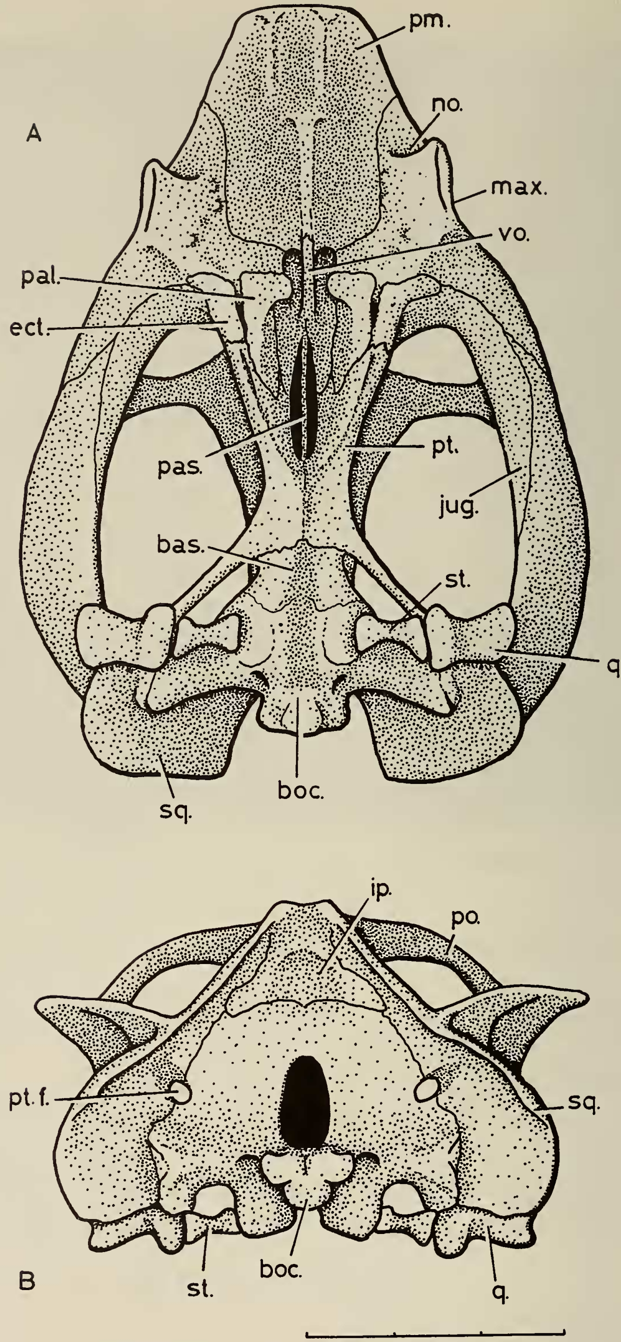

Fig. 23. *Diictodon testudirostris* SAM–10086. A. Skull in ventral view. B. Occipital view.

Locality

Gouph Tract, or Koup, Beaufort West district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon psittacops (Broom)

Dicynodon psittacops Broom, 1912: 869, pl. 92.

Type specimen

Skull and skeleton, AMNH 5534.

Locality

Beaufort West district, Cape Province.

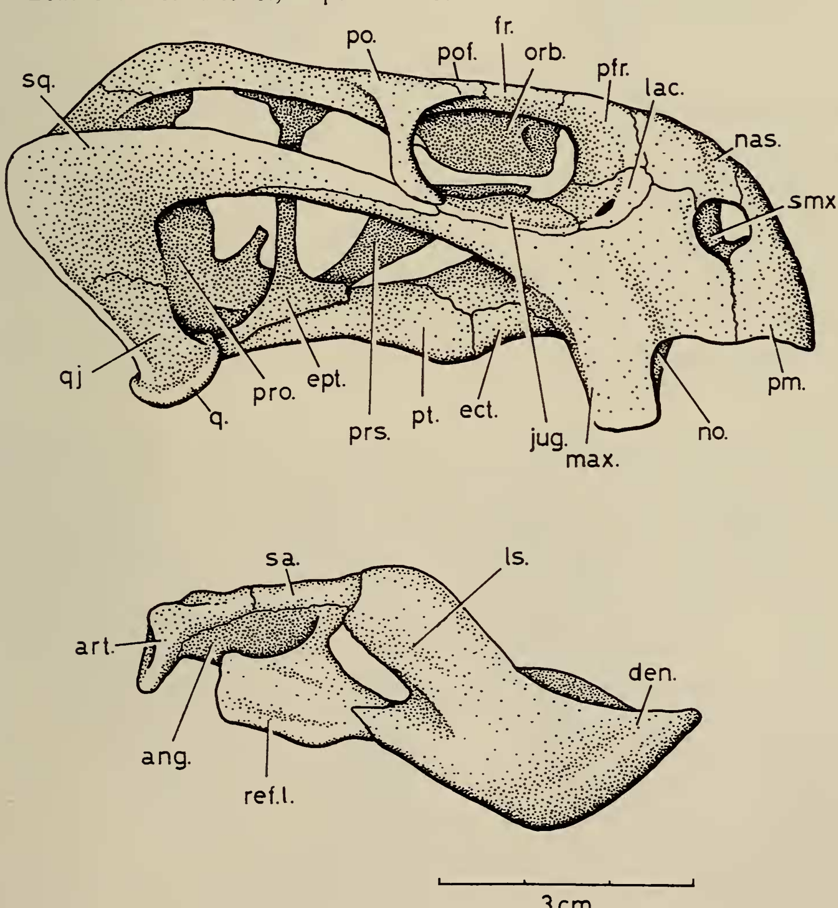

Fig. 24. *Diictodon testudirostris* SAM–10086. Skull and lower jaw in lateral view.

Horizon

Cistecephalus Zone.

Diictodon ictidops (Broom)

Dicynodon ictidops Broom, 1913: 466, figs 5–6.

Type specimen

Skull, AMNH 5510.

Locality

Beaufort West commonage, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon palustris (Broom)

Emydorhynchus palustris Broom, 1913: 456, fig. 19.

Type specimen

Skull, AMNH 5512.

Locality

New Bethesda, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Remarks

The type specimen, although poorly preserved, displays a sufficient number of characters to warrant its referral to *Diictodon*, which has page priority. Additional preparation of the type (TM 241) of *Emydorhynchus formosus* Broom, 1935*a* (mislaid at present, E.S. Vrba 1979 pers. comm.), will be needed to determine if this species should also be included in *Diictodon*.

Diictodon testudirostris (Broom & Haughton)

Dicynodon testudirostris Broom & Haughton, 1913: 36, pl. 7.

Type specimen

Skull, SAM–2354.

Locality

Dunedin, Beaufort West district, Cape Province.

Horizon

Cistecephalus Zone.

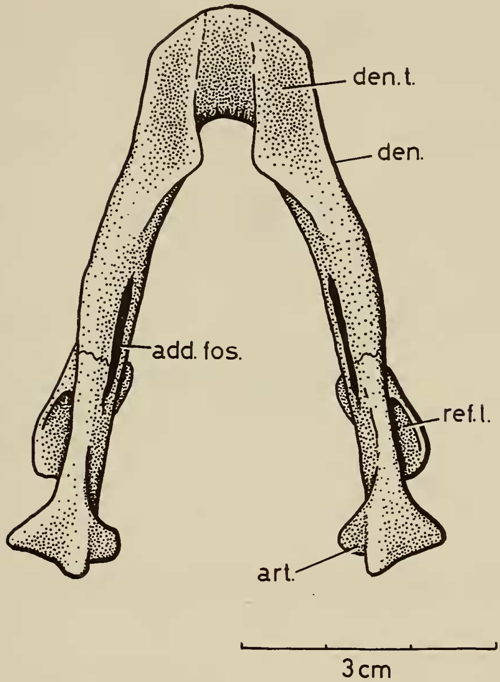

Fig. 25. *Diictodon testudirostris* SAM–10086. Lower jaw in dorsal view.

Fig. 26. *Diictodon testudirostris* SAM–10078. Stereophotograph of occlusal surfaces of upper and lower jaws. Scale: 5 cm.

Diictodon pygmaeus (Broom & Haughton)

Dicynodon pygmaeus Broom & Haughton, 1917: 123, fig. 23.

Type specimen

Skull, SAM–2664.

Locality

Dunedin, Beaufort West district, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon sollasi (Broom)

Dicynodon sollasi Broom, 1921: 648, figs 28–29.

Type specimen

Skull, SAM–7420.

Locality

Biesjiespoort, Victoria West district, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon macrorhynchus (Broom)

Dicynodon macrorhynchus Broom, 1921: 657, fig. 36.

Type specimen

Skull, BMNH R.4954.

Locality

New Bethesda, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Diictodon haughtonianus (Huene)

Dicynodon haughtonianus Huene, 1931: 186, fig. 25.

Type specimen

Skull, Institüt für Geologie und Paläontologie, University of Tübingen.

Locality

Blaauwkrans, Prince Albert district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon rubidgei (Broom)

Dicynodon rubidgei Broom, 1932: 189, fig. 62F.

Type specimen

Skull, BMNH 47081.

Locality

Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon nanus (Broom)

Diictodon nanus, Broom, 1936: 379, fig. 25A.

Type specimen

Skull, TM 268.

Locality

Houd Constant, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Diictodon grimbeeki (Broom)

Dicynodon grimbeeki Broom, 1935*a*: 7, figs 6–7.

Type specimen

Skull, TM 253.

Locality

Leeukloof, Beaufort West district, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon huenei (Broili & Schröder)

Dicynodon huenei Broili & Schröder, 1937: 118, figs 1–4.
Oudenodon huenei (Broili & Schröder) Toerien, 1953: 97.

Type specimen

Skull, University of Munich, 1934 vii 46.

Locality

La-de-da, Beaufort West district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon broomi (Broili & Schröder)

Dicynodon broomi Broili & Schröder, 1937: 132, figs 5–13.

Type specimen

Skull, University of Munich, 1934 viii 47a.

Locality

La-de-da, Beaufort West district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon grossarthi (Broili & Schröder)

Dicynodon grossarthi Broili & Schröder, 1937: 150, figs 14–18.

Type specimen

Skull, University of Munich, 1934 viii 48.

Locality

La-de-da, Beaufort West district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon whitsonae (Broom)

Dicynodon annae Broom, 1940*b*: 181, fig. 23.
Dicynodon whitsonae (Broom) Toerien, 1954: 937.

Type specimen

Skull, RC 42.

Locality

Wellwood, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon pseudojouberti (Boonstra)

Dicynodon pseudojouberti Boonstra, 1948: 60.

Type specimen

Skull, SAM–774.

Locality

Prince Albert Road, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon vanderhorsti (Toerien)

Dicynodon vanderhorsti Toerien, 1953: 91, fig. 60.

Type specimen

Skull, BPI 175.

Locality

Antjiesfontein, Prince Albert district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon antjiesfonteinensis (Toerien)

Dicynodon antjiesfonteinensis Toerien, 1953: 93, figs 61–62.

Type specimen

Skull, BPI 219.

Locality

Antjiesfontein, Prince Albert district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon tienshanensis (Sun)

Dicynodon tienshanensis Sun, 1973: 56.

Type specimen

Skull, in Institute of Vertebrate Palaeontology and Palaeoanthropology, Peking.

Locality

'Turfan Basin', Sinkiang Province, People's Republic of China.

Horizon

Lower Ko-Ko-Ya Group, Upper Permian.

Remarks

Cluver & Hotton (1979) pointed out that the specimen mentioned by Yuan & Young (1934) and described as *Dicynodon tienshanensis* by Sun (1973) can be referred to the genus *Diictodon*. The specimen in question is to date the only *Diictodon* recorded outside South Africa.

THE GENUS *KINGORIA* (Figs 27–30)

Kingoria Cox

Diagnosis

Medium-sized dicynodonts (average skull length 160 mm), jaws lacking teeth altogether or bearing a single pair of maxillary tusks. Parietals exposed between postorbitals behind parietal foramen. Septomaxilla recessed within opening of naris, maxilla rises high in side of snout to meet nasal. Low boss formed by nasal. Maxilla carries prominent caniniform process, palatal rim continued without interruption on to anterior blade of caniniform process. Rear of caniniform process extended as keel to level of ectopterygoid. Palatal portion of palatine very small, but making contact with greatly expanded premaxilla. Vomers form short septum in interpterygoid fossa, interpterygoid vacuity long and narrow. Ectopterygoid large, separating pterygoid from maxilla. Basipterygoid region constricted. Fused dentaries taper to form rounded anterior tip of lower jaw, no dentary tables present. Dorsal edge of dentary narrow, lateral dentary shelf widely expanded. Coronoid process weak or absent. Mandibular fenestra reduced or absent. Angular forms sharp ventral keel behind reflected lamina.

Kingoria nowacki (Huene)

Dicynodon nowacki von Huene, 1942: 156, fig. 2.
Kingoria nowacki (von Huene) Cox, 1959: 321.

Type specimen

Skull, Institüt für Geologie und Paläontologie, University of Tübingen, K–12.

Locality

Kingori, Tanzania.

Horizon

Kawinga Formation (Charig 1963).

Diagnosis

As for genus.

Discussion

A diagnosis of *Kingoria*, which has been fully described and characterized by Cox (1959), is provided only in the interest of completeness. Cox suggested that *Dicynodon galecephalus* Broom was related to or congeneric with *Kingoria*, but detailed examination of dicynodont type material shows that this is only one of a number of species previously included under *Dicynodon* which may be assigned to *Kingoria*. A potential problem of priority and nomenclature exists in that, on the basis of the poorly preserved type, *Dicynodontoides parringtoni* Broom, 1940*b*, appears to be related to or congeneric with *Kingoria*. In the

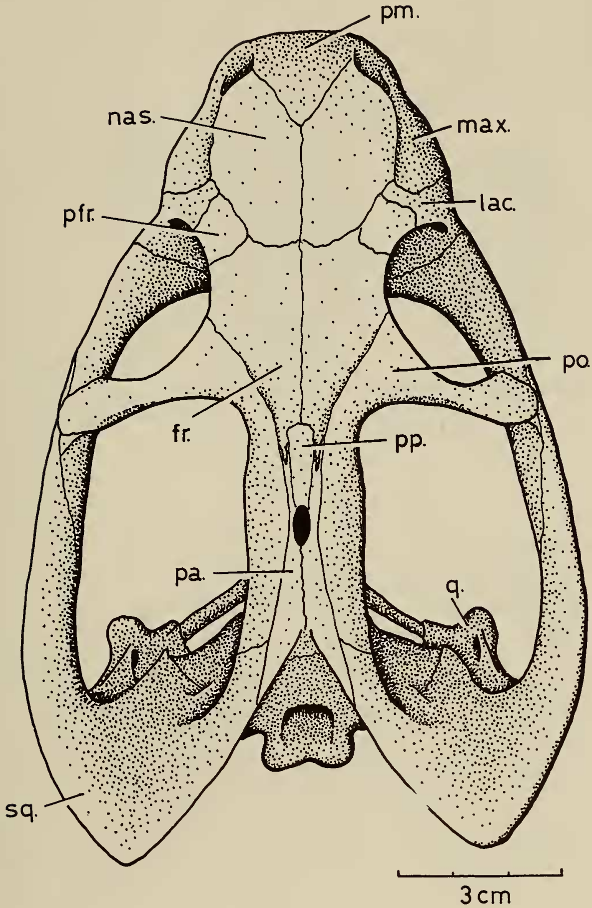

Fig. 27. *Kingoria nowacki*. Skull in dorsal view (after Cox 1959).

interests of stability, it is proposed that at this stage *Dicynodontoides* be retained as a separate genus, distinct from but related to *Kingoria*, until preparation of the type specimen (RC 45) allows a full comparison with the type of *Kingoria nowacki* to be made.

Kombuisia frerensis Hotton, 1974, from the lower Triassic *Cynognathus* zone, is the only Triassic form so far described that can be related to the upper Permian *Kingoria*.

Kingoria recurvidens (Owen)

Dicynodon recurvidens Owen, 1876: 46, pl. 69.

Type specimen

Skull, BMNH 40709.

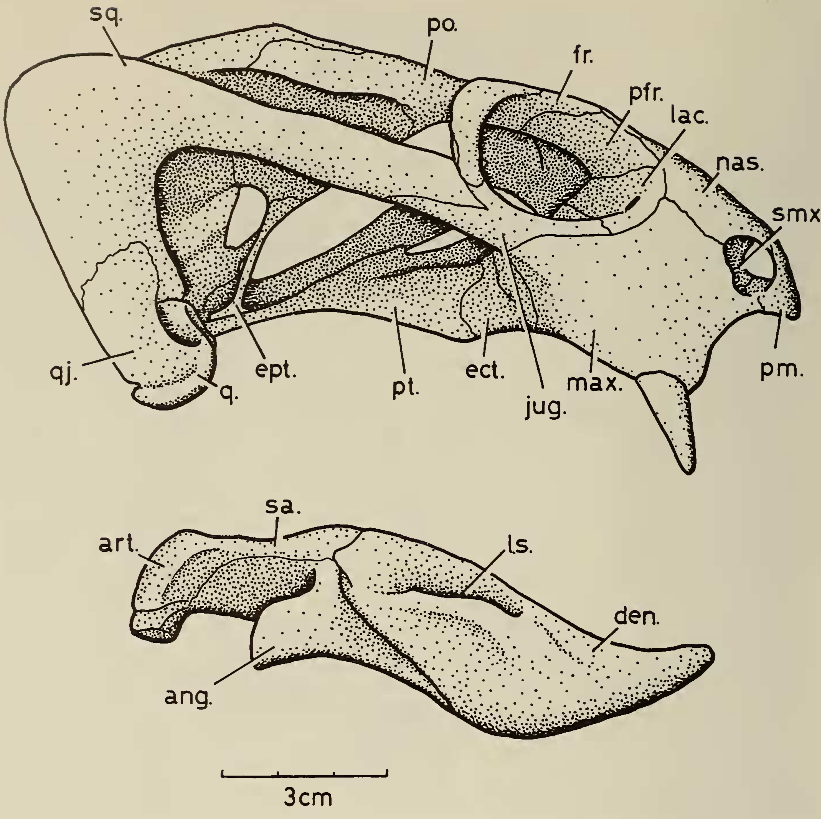

Fig. 28. *Kingoria nowacki.* Skull and lower jaw in lateral view (after Cox 1959).

Locality

Fort Beaufort, Cape Province.

Horizon

Cistecephalus Zone.

Kingoria gracilis (Broom)

Oudenodon gracilis Broom, 1901: 162.

Type specimen

Skull, SAM–590.

Locality

Pearston, Cape Province.

Horizon

Cistecephalus Zone.

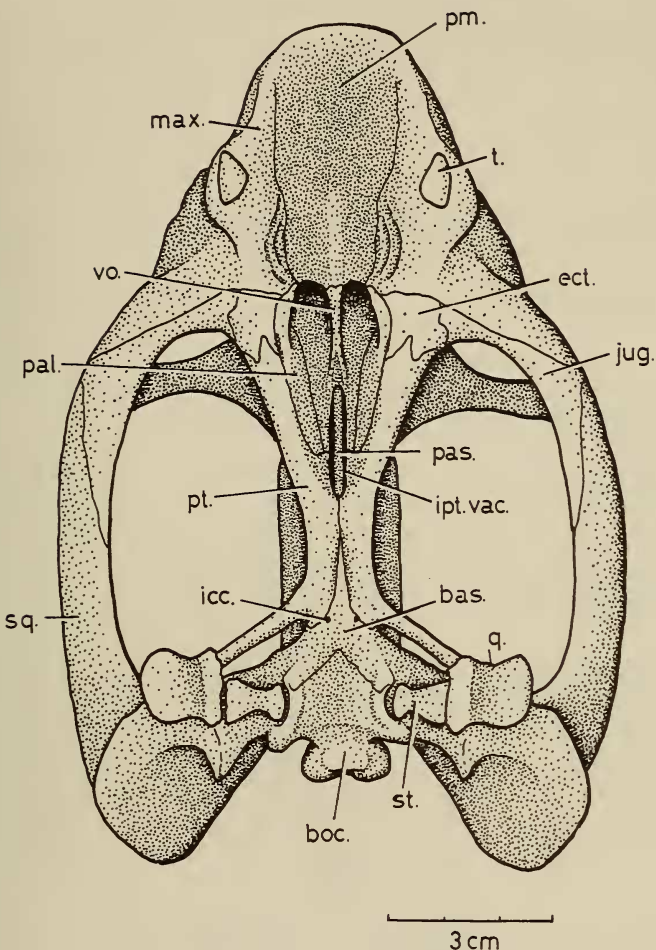

Fig. 29. *Kingoria nowacki*. Skull in ventral view (after Cox 1959).

Kingoria grahami (Broom)

Dicynodon grahami Broom, 1940*b*: 180, fig. 22.

Type specimen

Skull, RC 40.

Locality

St Olives, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone

Kingoria howardi (Broom)

Dicynodon howardi Broom, 1948: 604, fig. 22A.

Type specimen

Skull, RC 83.

Locality

Riversdale, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Kingoria duvenhagei (Broom)

Dicynodon duvenhagei Broom, 1948: 607, fig. 25.

Type specimen

Skull, RC 64.

Locality

Doornkloof, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

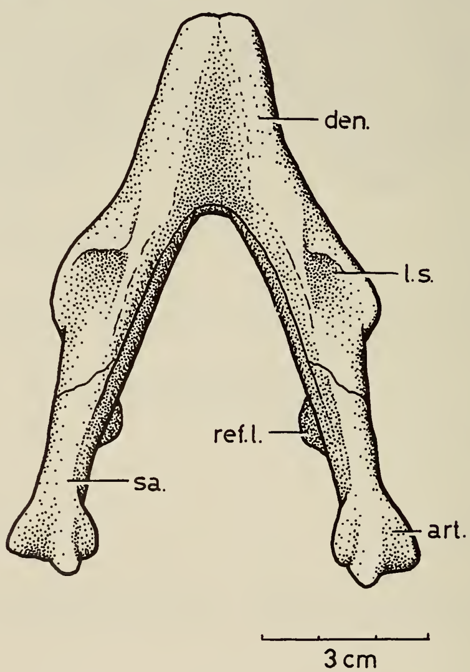

Fig. 30. *Kingoria nowacki*. Lower jaw in dorsal view (after Cox 1959).

Kingoria galecephala (Broom & Robinson)

Dicynodon galecephalus Broom & Robinson, 1948: 404.
Kingoria galecephala (Broom & Robinson) Cox, 1959: 324.

Type specimen

Skull, RC 97.

Locality

Ferndale, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

INTERRELATIONSHIPS OF *DICYNODON*, *OUDENODON*, *DIICTODON*, AND *KINGORIA*

Recognition of four central Permian dicynodont genera on the basis of the diagnoses given above has brought a clear picture of dicynodont interrelationships a step closer. While a full review of dicynodonts based on diagnoses of all genera cannot be attempted here, comparisons between *Dicynodon*, *Oudenodon*, *Diictodon*, and *Kingoria* nevertheless suggest closer relationships among some genera than among others (see Table 1).

In terms of lower jaw and palatal morphology, *Dicynodon* and *Oudenodon* resemble each other closely. It is unlikely that these similarities, involving dentary tables, a dorsal dentary sulcus, a deeply vaulted secondary palate with high palatal rim, and a large palatal development of the palatine, would have arisen as a consequence of convergence, and the differences which are seen in the palatal structure of the two genera are very likely the result of permanent loss of the maxillary tusk in *Oudenodon* and accompanying modification of masticatory function.

Diictodon resembles *Dicynodon* and *Oudenodon* in the presence of dentary tables, but the structure of the dorsal edge of the dentary as well as the palatal rim, caniniform process, and palatine sets the genus well apart from the others.

On the basis of palatal and lower jaw structure, *Kingoria* holds only a remote relationship with the other genera. The lower jaw, with flared lateral dentary shelves, blunt anterior tip, and highly reduced mandibular fenestra, is unique and, taken in conjunction with palatal structure, suggests an origin of the genus well separated from that of *Dicynodon*, *Oudenodon* or *Diictodon*.

Of the four genera discussed above, *Diictodon* has the greatest stratigraphic range. Specimens that can be referred to the genus are common in collections from the *Tapinocephalus* Zone, and are extremely abundant in certain *Cistecephalus* Zone localities. In addition, a specimen of *Diictodon* has been identified from the Upper Permian of Tienshan, China (Cluver & Hotton, 1979). The genus appears to persist to the very top of the *Daptocephalus* Zone, but has not been recorded from the Triassic Karoo formations. *Dicynodon*, *Oudenodon*, and

TABLE 1

Distribution of character states

	Dicynodon	*Oudenodon*	*Diictodon*	*Kingoria*
postcaniniform crest		×		
palatal rim continuous	×	×		×
palatal rim notched			×	
broad inter-temporal region		×		×
narrow inter-temporal region	×		×	
tusks present	×			
tusks absent		×		
tusks absent or present			×	×
dorsal sulcus in dentary	×	×		
dentary tables	×	×	×	
dentary tables absent				×
weak dentary shelf	×	×	×	
wide dentary shelf				×
septomaxilla recessed		×	×	×
septomaxilla exposed	×			
large palatine	×	×		
small palatine			×	×

Kingoria have not been identified from *Tapinocephalus* Zone localities, but all three are relatively common in the *Daptocephalus* Zone. *Oudenodon* appears to be better represented in *Cistecephalus* Zone localities than are *Dicynodon* or *Kingoria*, but whereas *Oudenodon* did not survive the Permian–Triassic transition, both *Kingoria* and *Dicynodon* can claim relationships with Triassic genera. *Kombuisia frerensis* (Hotton, 1974) is clearly a specialized relative of *Kingoria*, while the features that set *Dicynodon* apart from the other Permian genera are seen in modified form in *Lystrosaurus* and *Kannemeyeria* (Cluver 1971), as well as in many of the later, non-South African genera for which good descriptions exist (see Keyser & Cruickshank 1979). Future revision of the group of which *Dicynodon* is an early and primitive member will very likely show it to be geographically and stratigraphically the most wide-ranging dicynodont taxon.

Further speculation on the relationships of *Dicynodon*, *Oudenodon*, *Diictodon* and *Kingoria* would be fruitless before the status of other Permian dicynodonts has been clarified, in particular the pristerodontid genera and the primitive forms from the lowermost *Tapinocephalus* zone of the Beaufort series. However, recognition of the distinctive morphological features characterizing the four genera as set out above should aid materially in revealing what will undoubtedly prove to be a highly complex phylogeny of dicynodonts.

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Dr A. J. Charig, British Museum (Natural History), London, and Dr E. S. Gaffney, American Museum of Natural History, New York, are thanked for the loan of important type material in their care. The stereophotographs of *Oudenodon baini* (Fig. 14) and *Diictodon galeops* (Fig. 21) were taken by Messrs T. Parminter (British Museum (Natural History), London) and C. Tarka (American Museum of Natural History, New York) respectively. Other stereophotographs were taken by Mr N. J. Eden (South African Museum). Preparation of the South African Museum material illustrated in the text was largely the work of Mrs I. M. Chesselet, then of the Museum's Department of Palaeontology.

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ABBREVIATIONS

add. fos.	adductor fossa
ang.	angular
art.	articular
bas.	basisphenoid
boc.	basioccipital
bo.t.	basioccipital tuber
den.	dentary
den. s.	dentary shelf
den. t.	dentary table
ect.	ectopterygoid
eoc.	exoccipital
ept.	epipterygoid
for. mag.	foramen magnum
fr.	frontal
icc.	canal for internal carotid artery
ip.	interparietal
ipt. vac.	interpterygoid vacuity
itr.	intertuberal ridge
jug.	jugal
lab. fos.	labial fossa
lac.	lacrimal
lat. pal. f.	lateral palatal fenestra

l.s.	lateral shelf
max.	maxilla
no.	notch
op.	opisthotic
orb.	orbitosphenoid
pa.	parietal
pal.	palatine
pas.	parasphenoid
pcc.	postcaniniform crest
pfr.	prefrontal
pm.	premaxilla
po.	postorbital
pof.	postfrontal
pp.	preparietal
pro.	prootic
prs.	presphenoid
pt.	pterygoid
pt. f.	posttemporal fenestra
q.	quadrate
q.j.	quadratojugal
ref. l.	reflected lamina
sa.	surangular
smx.	septomaxilla
soc.	supraoccipital
sq.	squamosal
st.	stapes
t.	tusk
tab.	tabular
vo.	vomer
VIIf.	foramen for facial nerve
AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
BPI	Bernard Price Institute for Palaeontological Research, Johannesburg
RC	Rubidge Collection, Wellwood, Graaff-Reinet
SAM	South African Museum, Cape Town
TM	Transvaal Museum, Pretoria